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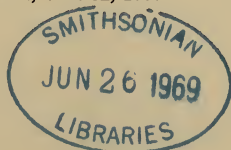
STUDIES ON SPIROBOLOID MILLIPEDS. VII.
A REMARKABLE NEW GENUS AND SUBFAMILY
OF THE SPIROBOLELLIDAE
FROM VERA CRUZ, MEXICO

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The milliped fauna of Mexico is, with continued exploration and study, rapidly assuming a position of world preeminence as regards its size and significance. The commingling of northern, tropical, and endemic elements has produced a diversity of novel and interesting millipeds that seems likely to yield exceptional finds for many decades to come, and the present total of about 400 species known from the country will quite likely be increased tenfold before the end is reached.

A major advance in our knowledge of Mexican diplopods was realized as one result of a prolonged collecting trip (July 1965 to September 1966) by Dr. G. E. Ball and Mr. Donald R. Whitehead, of the Department of Entomology, University of Alberta. Although primarily concerned with the capture of carabid beetles, these two entomologists devoted their time and energies to the accumulation of various other arthropods, and have very generously presented me with a magnificent collection of several thousand well-preserved millipeds taken in many of the Mexican states. Preliminary sorting reveals that the majority of the species represented, and many of the genera, represent undescribed taxa, and obviously many years will elapse before the material can be adequately studied and the results integrated with our present knowledge of Central American millipeds.

One specimen noted during sorting is of such special interest, however, that its immediate consideration is warranted as it



seems to belong to the spiroboloid family Spirobolellidae, previously unknown in Central America north of the Panama Canal Zone. The discovery of a new generic type in southern Vera Cruz is in itself important zoogeographically; moreover the species involved is of considerable interest because of several outstanding structural peculiarities.

FAMILY SPIROBOLELLIDAE BROLEMANN

Typhlobolellus new genus

Type species: *T. whiteheadi*, new species.

Diagnosis: A spirobolellid genus characterized by the absence of ocelli, by the origin of the ozopores on the 3rd segment, by the cristate modification of the basal podomeres, by the formation of a sympleurotergal bridge behind the metasterna, and by the retention of sclerotized sternal structures in association with the phallopods. The first four characters mentioned are unique within the order Spirobolida; the second, furthermore, is unique within the Diplopoda.

Distribution: Southern Vera Cruz, near sea level.

Typhlobolellus whiteheadi new species

Figures 1-8

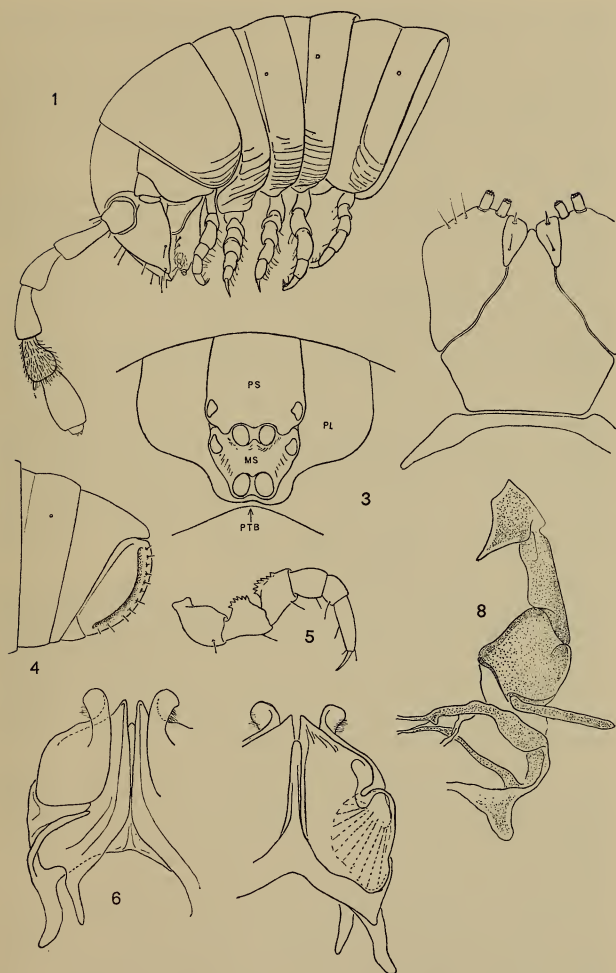
Holotype: Adult male, deposited in the USNM, from sea-level swamp forest, 0.8 miles west of Sontecomapan (ca. 11 miles north of Catemaco), Vera Cruz; 18 September 1965, G. E. Ball and D. R. Whitehead, collectors.

Length about 28 mm. (specimen broken), body slightly compressed, transverse diameter ca. 1.3 mm., vertical diameter ca. 1.4 mm. at midbody; general appearance remarkably slender for a spiroboloid and more similar to that of a cambaloid, the W/L ratio 4.9 percent. Body with 55 segments, the last two legless.

Head of the form shown in Figure 1, smooth and polished, with a few randomly dispersed facial setae and 2-2 clypeal setae. No trace of ocelli. Parietal sclerite small, subtriangular, but clearly distinct. Basal segment of mandible moderate in size, vertically elongated; distal segment much smaller than usual for the order, extending less than half the length of

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FIGS. 1-8. *Typhlobolellus whiteheadi* n. sp. 1, head and first six body segments, lateral view. 2, gnathochilarium. 3, ventral region of midbody segment, ventral aspect, legs removed; PS: prosternum; MS: metasternum; PL: right pleuron; PTB: pleurotergal bridge isolating metasternum from caudal edge of segment. 4, posterior end of body, lateral aspect (legs not shown). 5, leg from midbody segment showing modification of prefemur and femur, and reduced setation. 6, coleopods,



posterior aspect. 7, coleopods, anterior aspect. 8, left phallopod and associated sternal structures, posterior aspect. Drawings from male holotype. Figures 1 and 3 originally made with magnification of 45 \times , the others 90 \times .

genal edge. Gnathochilarium as figured (Fig. 2), no separate cardine sclerites observed.

Antennae remarkably long and slender, extending back to 6th segment when appressed to body, individual antennomeres cylindrical or very slightly compressed (especially distally), moderately clavate, the 6th article largest and subfusiform; 7th small, discoid, with four minute terminal sensory cones. No special sensory setae or areas observed on other articles.

Collum (Fig. 1) smooth and polished, laterally broadly rounded and narrowly margined along anterior edge up to level of craniomandibular articulation; surface of lateral ends with several indistinct longitudinal striations.

Segments of body essentially similar in structure; each prominently constricted at midlength producing two subsegments of virtually equal diameter, but since telescoping of the successive segments is only moderate, the body profile is distinctly submoniliform. Deepest part of each constriction with a sharp-edged transverse suture line marking anatomically the union of prosomite and metasomite, the latter apparently not subdivided into mesozonite and metazonite as in most other spiroboloid families. Traces of dorsolateral longitudinal sutures discernable just behind ozopores with suitable illumination; other segmental sutures obliterated. Surface of segments smooth and polished, microscopically reticulated; lower parts of metasomites with several indistinct longitudinal striations. Ozopores small but distinct, located at about the midlength of each metasomite of segments 3 through 54.

Pleurosternal structure (Fig. 3) unusual in that the metasterna do not form the ventral part of caudal edge of segment, but are enclosed by medially projecting and coalesced elements of both the pleural sclerites and ventral ends of the metasomites, forming a "sympleurotergal" bridge similar to that of the 7th segment of males in other spiroboloid families. Anterior sternum slightly convex, finely and densely punctate; posterior sternum flat, smooth except for a few microscopic striations. Pleural sclerites smooth, their sutures clearly visible in dry material.

Posterior segments (Fig. 4) not especially telescoped, the last produced into a moderate-sized, cuneate epiproct which does not entirely conceal the paraprocts in dorsal aspect; latter strongly convex, smooth, the medial margins inflated and set off by prominent basal grooves, each with a marginal series of 11 or 12 conspicuous setiferous tubercles. Hypoproct transversely triangular, flat and smooth, without peculiarities.

Legs (Fig. 5) short, not visible from above when extended laterally, differing from those of all other known spiroboloids in that the prefemora and femora are strongly convex dorsally, with a median row of about six acute declivent spines. Ventral setae of midbody legs reduced: 1-1-1-1-1-1, usually a small dorsal seta at end of tarsal segment and an even smaller one ventrally at base of tarsal claw. Anterior legs without coxal lobes or other modifications, the tarsal claws elongate and slender.

Ventral side of 7th segment continuous across a sympleural bridge, but

without any modification of the median, postgonopodal area, the surface merely flat and undistinguished. Gonopods basically similar to those of *Spirobolellus* and related genera. Coleopods (Figs. 6, 7) with well-defined transverse sternum, medially produced into an elongate, digitiform process; coxae with prominent deep notch along ventrolateral edge in front of lateral articulation of telopodite; telopodites of moderate size, separated on the posterior side from the median prolongation of the sternum by a narrow lobe of the coxa; distally lobed, each lobe with a subterminal row of fine setae along the outer edge.

Phallopods (Fig. 8) similar to those of other spirobolellids in general form, attached to a delicate but prominent sternal structure, heretofore not recorded for this family; gonopod divided by an oblique suture into a broad, subquadrate coxal remnant and a more slender and elongated telopodite, the latter also divided (secondarily?) into a basal slender trunk and a broad, laminate, triangular distal lobe set at right angles. Coxa with slender apodemes attached at midlength of its ventral edge as usual for the family. No trace of grooving or glandular modification noted in the thin, flattened, and delicate phallopods.

Color pattern faded through preservation, but generally pale testaceous brown with metasomites distinctly darker, imparting an annulated appearance, the pigmentation more intense on caudal third of body; last segment and paraprocts nearly blackish. Head, antennae, legs, and lower sides pale yellow.

GENERAL OBSERVATIONS

1. Trypsin as a clearing agent. The small size of the type specimen of *T. whiteheadi* and obvious delicacy of its structure required special techniques for preparation prior to study. The use of KOH as a macerating material, while suitable for large and robust diplopods, seemed too hazardous in this case, so that removal of muscle tissue and internal organs was accomplished by breaking the specimen between body segments 7 and 8, and soaking the anterior end of the body overnight in an aqueous solution of commercial C.P. trypsin at a temperature of approximately 100° F. The use of this technique is recommended to the attention of other students of small and fragile arthropods. All of the non-sclerotized tissue can be digested and washed out without any damage to even the most delicate sclerotized structures, something that can not be asserted for caustic agents even with dilute solutions and moderate warming.

2. Phallopod sternum. The discovery of a fairly extensive sternal remnant to which the posterior gonopods are attached is of considerable interest from the standpoint of phylogeny. Unfortunately the structure was unknowingly damaged during dissection, so that the drawings show a somewhat distorted appearance. There seems to be both transverse elements and proximally directed apodemes (= tracheal apodemes?), and if the latter possibility can be confirmed by future studies, a new light will be shed upon the homology of the phallopod basal apodemes

in other spiroboloid groups. The presence of sternal elements connected with the phallopods, of course, can only be considered as plesiomorphic in character.

3. Notes on the classification of the Spirobolellidae. When first set up by Brolemann in 1913, this family contained only three genera. In my opinion, there are now no less than 16 nominal generic taxa here referable, many of course being of quite dubious validity.

Although Brolemann defined his family groups with considerable precision, later workers either ignored the family category in the Spirobolida altogether (Chamberlin, Verhoeff), or combined the Spirobolellidae with the Spirobolidae (Attems, Carl). As there has been no synopsis of the family since 1914, it certainly seems important to list here the generic names that have been based upon taxa agreeing with Brolemann's diagnosis and to propose some disposition of their taxonomic status. Full literature citations may be extracted from the recent list (Hoffman & Keeton, 1960) of generic names in the Spirobolida.

<i>Aporobolus</i> Loomis, 1934	Tobago
<i>Attemsobolus</i> Verhoeff, 1924	Australia
<i>Barrobolus</i> Chamberlin, 1925	Panama
<i>Carlobolellus</i> Brolemann, 1931	New Caledonia
<i>Desmocerellus</i> Attems, 1953	New Zealand
<i>Howeobolus</i> Verhoeff, 1928	Lord Howe Island
<i>Mauritobolus</i> Verhoeff, 1939	Mauritius (native?)
<i>Microspirobolus</i> Silvestri, 1898	Venezuela
<i>Paraspirobolus</i> Brolemann, 1902	Brasil
<i>Physobolus</i> Attems, 1936	India
<i>Poratobolus</i> Verhoeff, 1924	Australia
<i>Queenslandobolus</i> Verhoeff, 1924	Australia
<i>Sechellobolus</i> Brolemann, 1913	Seychelles (native?)
<i>Spirobolellus</i> Pocock, 1894	Sumatra
<i>Spirobolinus</i> Silvestri, 1898	Ecuador
<i>Walesbolus</i> Verhoeff, 1928	Australia

The taxonomy of the foregoing ensemble is at present quite unsatisfactory. Brolemann's concept of *Spirobolellus* was based upon *S. rainbowi* Brol., an Australian species, whereas the type of the genus, *S. chrysodirus* Pocock, was from Celebes and its gonopod structure was not accounted or figured. Inferentially, however, it seems highly probable that the two species are congeneric, as there is now known a fairly large group of similar species ranging from Sumatra to Micronesia and south to New Caledonia, Australia, and New Zealand. J. Carl (1926) has given a good account of the Caledonian fauna and remarked, quite correctly in my opinion, that many if not all of Verhoeff's 1924 generic names are really based only on species characteristics. What Carl did not take into account, nor has anyone else more recently, is that a generic separation between the Indoaustralian taxa referred to *Spirobolellus*, and those of the New World to *Microspirobolus*, appears impossible. Aside from

literature accounts, I have compared some specimens from the Caroline Islands with Haitian material, and can find no justification for the recognition of two genera.

The name *Microspirobolus* has been used for a large number of Neotropical, chiefly Antillean, species, but here again the type species was described without reference to its gonopod structure so that the exact status of *M. pulchellus* remains a little dubious. But in this case, Silvestri later asserted that the two new species *M. marmoratus* and *M. insularis* (1908), which were well-described and illustrated, are congeneric with *pulchellus*, and Silvestri rarely if ever overlooked possible generic distinction.

The generic name *Barrobolus* has already been combined with *Microspirobolus* by Loomis (1964). I have briefly considered the status of the two names *Aporobolus* and *Spirobolinus* in 1955 without reaching a definite conclusion; both nominal taxa lack ozopores on the 7th segment but are otherwise typical spirobolellids. I here retain the two names but have no illusions about a long life for either of them.

Paraspirobolus was based upon immature males of a species that has not been reported since 1902 and remains something of an enigma. Schubart (1947) suggests that *P. paulistus* Brol., the type and only species, was based upon specimens of *Sechellobolus dictyonotus* (Latzel) which is synanthropically not rare in southern Brasil. I agree entirely with this possibility as there is no reason to believe that an endemic spirobolellid genus occurs in that part of South America. *Sechellobolus* (misspelled *Seychellobolus* by several authors) itself seems to contain only its type species *S. dictyonotus* (Latzel), which is known from Berlin and Hamburg (the type locality!), the Seychelles, Mauritius, and Brasil. I have personally identified specimens also from Jamaica, and believe that the milliped described from Annam by Graf Attems (1953) as *Physobolus striatus* is the same form. In view of such a far-flung distribution, the relative paucity of records is surprising, and the original home of the species has yet to be ascertained.

Assuming the probable correctness of the synonymies mentioned above, we find that *Paraspirobolus* is the older of the two generic synonyms, while *dictyonotus* (Latzel, 1895) is the oldest of several specific names that seem to have been based upon the same species. In most respects this genus is similar to *Spirobolellus* but can be distinguished on the basis of what appears to be a receptacle (seminal?) in the telopodite of the phallopod.

Attemsobolus is likewise weakly differentiated, its type species is marked chiefly by the presence of a secondary process on the coleopod telopodite (Verhoeff wrote that the telopodite was deeply *bifid!*). *Howeobolus* and *Walesbolus* are not well-described, the gonopods apparently having been torn apart before the drawings were made, but the names may be retained provisionally.

Physobolus, however, appears to be a well characterized genus with two species in the "Farther India" region. The sternum of the coleopods

is small and transverse, leaving the coxal plates entirely exposed; the phallopod seems to be two-segmented with a distinct gland located in the basal (coxal?) division.

Taking the foregoing remarks collectively, it is possible to render the list of generic names into a somewhat more condensed roster, and to align them in three groups which can be considered as subfamilies for the present. I believe that the suggested subordination of six names constitutes new synonymy in each case. Characteristics of the subfamilies can be readily derived from those of the included genera, the Spirobolellinae for instance includes all of the species that lack the specialized features of *Physobolus* and *Typhlobolellus*. Of these last two genera, *Typhlobolellus* is by far the more disjunct, and may well warrant family status in the light of future investigations.

The proposed classification may be rendered thus:

FAMILY SPIROBOLELLIDAE BROLEMANN, 1913

SUBFAMILY SPIROBOLELLINAE, n. SUBFAM.

Spirobolellus Pocock, 1894 (syns. *Barrobolus* Chamberlin, 1925, *Mauritobolus* Verhoeff, 1939, *Microspirobolus* Silvestri, 1898, *Porotobolus* Verhoeff, 1924, *Queenslandobolus* Verhoeff, 1924). East Indies, Micronesia, New Caledonia, eastern Australia; Panama, Colombia, Ecuador, Peru, Venezuela, West Indies (except Jamaica!).

Aporobolus Loomis, 1934. Tobago. (= *Spirobolinus*?).

Attemsobolus Verhoeff, 1924. Queensland.

Carlobolellus Brolemann, 1931. New Caledonia.

Desmocricellus Attems, 1953. New Zealand.

Howeobolus Verhoeff, 1928. Lord Howe Island.

Paraspirobolus Brolemann, 1902 (syn. *Sechellobolus* Brolemann, 1913). Widely dispersed by commerce, perhaps endemic in south-east Asia.

Spirobolinus Silvestri, 1898. Ecuador.

Walesbolus Verhoeff, 1928. New South Wales.

SUBFAMILY PHYSOBOLINAE, n. SUBFAM.

Physobolus Attems, 1936. Northern India; Vietnam.

SUBFAMILY TYPHLOBOLELLINAE, n. SUBFAM.

Typhlobolellus, n. gen. Southern Mexico.

4. Some notes on distribution and relationships. The presently known distribution of the Spirobolellidae is especially interesting; in the main

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FIG. 9. Distribution of the family Spirobolellidae (broken line) and the family Atopetholidae (cross-hatching). The type locality of *Typhlobolellus whiteheadi* is indicated by the black spot in southern Mexico. Records for the family in the Indian Ocean (Seychelles, Mauritius) are presumed to be due to accidental introduction through com-



merce. The two areas circled on the mainland of southeast Asia indicate the occurrence of the two known species of *Physobolus* and the subfamily Physobolinae. With the foregoing exceptions the distribution of *Spirobolellus* is virtually co-extensive with that of the family.

points it agrees closely with that of the Rhinocricidae although less extensive. The map (Figure 9) shows in a general way the occurrence of spirobolellids as here understood. The greatest numbers of species are to be found on islands, such as New Caledonia (25) and Hispaniola (10), remarkably few are so far known from continental regions (south-east Asia, northern South America). Perhaps this reflects a declining evolutionary status for the group. Geographic ranges shared between the East and West Indies are not to be explained by recourse to "drift" or other postulated crustal movements unless we can suppose that ancestral forms occurred widely across a single northern continent ("Laurasia") in the Palaeozoic, prior to the formation of the Atlantic Ocean and prior to contact between the two subsequent northern landmasses with South America and Africa, respectively.

As already pointed out some years ago (Hoffman & Orcutt, 1960, p. 112), the family most closely related to the Spirobolellidae appears to be the North American endemic group Atopetholidae, the present range of which is shown by cross-hatching on the map. On the basis of gonopod structure, one might suspect that the atopetholids are perhaps somewhat more primitive, but speculations of this sort are still quite premature.

Doubtless the Rhinocricidae is to be regarded as belonging to the same group of families. Although rhinocricids do extend into Brasil and Argentina, all of the far-southern species are quite homogeneous and the center of diversification in this family is located in northern South America and the West Indies. Antipodal vicariation at the generic level is to be noted between *Rhinocricus* (Haiti, Porto Rico, Cuba) and *Acladocricus* (Indoaustralian region generally), and between *Neocricus* (Venezuela, Colombia) and *Dinematocricus* (Australasia).

One inference to be drawn from the foregoing remarks is that the two families Rhinocricidae and Spirobolellidae originated in the northern hemisphere and have invaded South America (during the late Mesozoic or, perhaps, later, early Pliocene) only very slightly; neither group is represented in temperate eastern Asia, the Indian peninsula, or in Africa. Probably the present distribution of spirobolellids is due to their virtual displacement on continental areas by members of more modern and/or successful families (e.g., Atopetholidae and Rhinocricidae), although the mechanics of competition and displacement among milliped groups have yet to be demonstrated factually.

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